RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Litter removal increases plant diversity by promoting both native and exotic forbs in heavily invaded coastal sage scrub in Southern California, U.S.A.

Advyth Ramachandran[1,2,3,4], Caryn D. Iwanaga[1,2,5], Michael Fugate[1], Jared D. Huxley[1,2], Annika Rose-Person[1,2,6], Rhea Amatya[1,2], Thuy-Tien Bui[1,2,7], Marko J. Spasojevic[1,8]

Litter produced by exotic grasses is known to negatively impact native species through multiple mechanisms. While litter removal is a potential restoration tool to recover native species, the effects of litter removal on overall plant community structure are not well understood as most studies focus on native species recovery. In a litter removal experiment in Southern California, U.S.A., we found that plant communities receiving litter removal treatment differed in species composition from control plots and had 4.4% higher native forb relative abundance and 7.0% higher exotic forb relative abundance, on average. These changes in exotic and native forb abundance with litter removal altered community structure by increasing overall Shannon diversity, while only having a modest positive effect on overall species richness. In contrast, we found no effect of litter removal on the species richness or Shannon diversity of native species. Taken together, these findings suggest that in herbaceous systems litter removal is likely to alter community composition primarily by increasing the abundance of native and exotic forbs already present in the community, rather than by allowing the establishment of new native species. Our study adds to a growing body of literature demonstrating that litter produced by exotic grasses inhibits native forbs in California grasslands and coastal sage scrub and highlights a potential trade-off between controlling exotic grass invaders and controlling exotic forb invaders. If managing for increased species diversity is the goal, litter removal may be an appropriate intervention to move plant communities toward a more diverse state.

Key words: **California annual grassland, California coastal sage scrub, community structure, invasion, residual dry matter, restoration, species diversity, thatch**

Implications for Practice

- In California coastal sage scrub (and likely similar systems such as California annual grasslands), litter removal via raking can be an effective strategy to increase native forb abundance, but also increases exotic forb abundance.
- By promoting the growth of native forbs already present and co-occurring with invasive grasses, litter removal can increase the abundance of native forbs even without seed addition.
- Litter removal can present a trade-off between controlling exotic grass invaders and controlling exotic forb invaders; however, if managing for higher species diversity is the management goal, litter removal may be an appropriate intervention.

Introduction

Invasive plant species are a significant problem for ecosystem management globally, often reducing local biodiversity and altering ecosystem processes (Vilà et al. 2011; Pyšek et al. 2012). Many ecological restoration projects aim to control the impacts of invaders in an effort to increase the abundance of native species. To design successful interventions to promote native species, an understanding of the mechanisms by which invasive species reduce native species success is critical. One well-known mechanism

---

Author contributions: AR, CDI, MF, JDH, AR-P, MJS, RA, T-TB designed the study; AR, CDI, MF, RA, JDH, ARP collected the data; AR, CDI, T-TB, RA processed the data; AR analyzed the data; AR wrote the manuscript with edits from all authors.

[1] Department of Ecology, Evolution, and Organismal Biology, University of California–Riverside, 2710 Life Science Building, Riverside 92521, CA, U.S.A.
[2] Center for Conservation Biology, University of California—Riverside, 1435 Boyce Hall, Riverside 92521, CA, U.S.A.
[3] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, 1900 Pleasant Street, 334 UCB, Boulder 80309, CO, U.S.A.
[4] Address correspondence to A. Ramachandran, email advyth.ramachandran@colorado.edu
[5] Department of Biology, Institute of Ecology and Evolution, University of Oregon, 272 Onyx Bridge, 5289 University of Oregon, Eugene 97403, OR, U.S.A.
[6] Department of Biology, Gonzaga University, 502 E. Boone Avenue, AD 5, Spokane 99258, WA, U.S.A.
[7] Bren School of Environmental Science and Management, University of California—Santa Barbara, 2400 Bren Hall, Santa Barbara 93106, CA, U.S.A.
[8] Environmental Dynamics and GeoEcology Institute, University of California—Riverside, 2460 Geology Building, Riverside 92521, CA, U.S.A.

doi: 10.1111/rec.14340
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14340/suppinfo

by which invasive plant species impact other co-occurring species, including natives, is the production of litter (D'Antonio & Vitousek 1992; Eppinga et al. 2011; Wainwright et al. 2017). Persistent litter layers produced by invasive species, often grasses, can alter species composition, vegetation structure, and ecosystem functioning (Facelli & Pickett 1991; Loydi et al. 2013; Kortessis et al. 2022). Litter can reduce the establishment and growth of co-occurring species by reducing light availability (Foster & Gross 1998; Molinari & D'Antonio 2020), hindering dispersal by trapping seeds (Ruprecht & Szabó 2012), altering the fire regime (D'Antonio & Vitousek 1992; Hernández et al. 2019), promoting disease (Benitez et al. 2022), depositing allelopathic compounds into soil (Loydi et al. 2015), and/or altering nutrient availability (Farrer & Goldberg 2009; Chen et al. 2018). These effects of litter can produce a positive feedback loop where litter deposition further promotes the growth of the litter-producing grasses (Lenz et al. 2003; Mariotte et al. 2017; Molinari & D'Antonio 2020), potentially resulting in extensive invasion, type conversion from shrubland to grassland (D'Antonio & Vitousek 1992; Wolkovich et al. 2010), and the creation of alternative stable states resistant to restoration efforts (Cox & Allen 2008).

In systems where litter is a primary mechanism by which exotic grasses suppress native plant species, litter removal may be an effective strategy to promote native species recovery. However, while removal of exotic plant litter has been demonstrated to positively impact native species (Foster & Gross 1998; Coleman & Levine 2007; Brandt & Seabloom 2012), our understanding of the effects of litter on native versus exotic species is limited (Loydi et al. 2013). Litter removal may promote both native and exotic species by favoring species with functional strategies that do not confer tolerance to dense litter. For example, forb species with relatively low tolerance for low-light conditions may benefit more from litter removal than species with an upright growth form and higher tolerance for low-light conditions, a strategy which can allow persistence in litter-dense grasslands (Molinari & D'Antonio 2014, 2020). Forbs with resource-acquisitive functional strategies may benefit more from litter removal than forbs with conservative strategies, due to the greater negative influence of litter-induced light limitation on seed production and germination in acquisitive species (LaForgia 2021).

Such responses may lead to species turnover, with potentially important consequences for land management. For instance, if light-limited, resource-acquisitive species can disperse to sites following litter removal, these species may replace shade-tolerant species. If litter removal promotes the recruitment or growth of exotic species, and those species are competitively superior to natives in the absence of litter due to having, for example, earlier germination and rapid growth (such as the case of exotic versus native forbs in California; Eviner 2016; Minnich 2008), litter removal could simply lead to a replacement of invasive grasses by other exotic species. In this case, litter removal would not promote native species that may be the targets of management. Alternatively, if resource-acquisitive species are dispersal-limited, litter removal may simply increase the recruitment and growth of shade-tolerant native and exotic species already present and coexisting with invasive litter-producing grasses.

Importantly, the result of these differential species responses to litter leads to multiple potential alternative states for community-level biodiversity in response to litter removal. By increasing species richness, evenness, or causing species turnover, litter removal could cause a net change in species diversity. Critically, understanding which of these scenarios will occur with litter removal is important for management as some of the possible community states may be considered undesirable depending on the management goal. For example, a small increase in native forbs but large increase in exotic forbs with litter removal may be undesirable if the goal is to support pollinators that depend on native forbs. Therefore, understanding how litter removal affects overall community structure, including both native and exotic species abundance, can give land managers a richer picture of the effectiveness of this restoration tool.

To improve our understanding of the effects of litter removal on community structure, we conducted a litter removal experiment in a heavily invaded coastal sage scrub (CSS) ecosystem in Southern California, U.S.A., which can contain a sizeable native forb component and a diverse set of exotic forbs (Cleland et al. 2016). CSS provides a dramatic example of widespread invasion by litter-producing exotic grasses (Minnich & Dezzani 1998). CSS was historically composed of a matrix of native short-statured drought-deciduous subshrubs and native annual forbs (Rundel 2007). CSS, like many other California ecosystems with a substantial herbaceous component such as grasslands and forblands, experienced widespread invasion by exotic annual grasses beginning in the 18th century (Minnich 2008; Cleland et al. 2016; Eviner 2016). These invasive grasses grow in the winter wet season (October–April) and produce a thick litter layer that persists during the summer and fall months (Cleland et al. 2016; Eviner 2016). Multiple studies have demonstrated that light limitation induced by this litter layer is the dominant mechanism by which invasive grasses reduce the success of native species in CSS and other California herbaceous systems (Amatangelo et al. 2008; Mariotte et al. 2017; Chen et al. 2018). While the primacy of litter accumulation in driving grass invasion is well-established, relatively little work has investigated the effects of litter removal on overall community structure. In this study, we examine how litter removal affects plant community diversity and composition. Specifically, we test the following hypotheses:

H1: Litter removal increases native forb and exotic forb abundance, richness, and diversity, which drives increases in overall community species richness and diversity.

H2: Litter removal shifts community composition toward a state with more native forbs and exotic forbs.

We tested these hypotheses using a Before-After-Control-Impact (BACI) design, where we first measured baseline species composition before any experimental manipulation and then removed litter in treatment plots for 2 years. To assess the effects of litter removal on functional group (i.e., native forb and exotic forb) abundance, species diversity, and species composition, we compared changes over time in control plots to changes in litter removal plots. This experimental design allowed us to quantify the effects of litter removal on community composition and diversity over background interannual variation, allowing us to draw stronger inferences as to whether litter removal is an effective tool to restore native plant communities.

Methods

Study Site

The experiment was located at a site on the University of California–Riverside campus in Riverside, California, U.S.A. (33.967°N, 117.323°W) where the mean annual temperature is 19°C and the mean annual precipitation is 238 mm (30-year climate normal for the city of Riverside; National Centers for Environmental Information 2023). The site is at 400 m above sea level and is a north-facing slope that was formerly composed of Riversidean CSS (Cleland et al. 2016) dominated by native subshrubs *Artemisia californica* (California sagebrush; Asteraceae), *Encelia farinosa* (brittlebrush; Asteraceae), *Salvia mellifera* (black sage; Lamiaceae), *Salvia apiana* (white sage; Lamiaceae), *Acmispon glaber* (deerweed; Fabaceae), and *Eriogonum fasciculatum* (California buckwheat; Polygonaceae). These native subshrubs are present in small, scattered stands in the adjacent south-facing slopes but not at the experiment site. The experiment site is now an exotic annual grassland dominated by the invasive annual grass *Bromus diandrus* (ripgut brome; Poaceae) with interspersed exotic and native forbs. All taxonomic names in this article follow the Jepson Flora (Jepson Flora Project 2024).

Experimental Design

In 2021, we established eighty 3 × 1.5 m experimental plots which were assigned treatments in a paired design with blocks containing two plots each, where one plot received litter removal via raking with soil rakes, while the other was left as an unmanipulated control (40 blocks total). The plots were arranged in a grid pattern of alternating litter removal and control plots (Fig. S1). These plots were previously used to conduct a litter removal experiment for teaching an undergraduate lab course from 2008 to 2015. To assess whether this legacy of use had any persisting effects, we collected baseline species composition in the spring of 2021 prior to conducting our experiment and compared community structure in historically raked versus historically unmanipulated plots. Treatments were assigned to plots (Fig. S1) in an identical fashion to those assigned in the 2008–2015 experiment (i.e., a plot that had litter removed from 2008 to 2015 also had litter removed in our experiment). Plots that we designated as controls (no litter removal) have never experienced experimental litter removal. We acknowledge that due to the past use at the site and the potentially long-lived nature of annual forb seeds in this system, there is a possibility that the seedbank of historically manipulated plots differs from that of the historically unmanipulated plots. However, as the plots are small, only 1 m apart, and arranged in an alternating grid pattern, it is highly likely that species could disperse among the plots during the previous manipulations. Additionally, as all plots were unmanipulated for 7 years before our experiment, there has likely been sufficient time for equilibration of composition among plots in this annual system.

We removed litter using soil rakes in the fall (September/October) of 2021 and 2022 before the onset of the rainy season (late October–May) and took care to avoid soil disturbance. Recumbent (defined as litter laying on the soil surface) and standing (defined as senesced grass matter still rooted in soil) litter was collected and removed from the plots; however, deeply rooted standing senesced grasses and small fragments of litter at the soil surface were not removed to avoid causing soil disturbance (Fig. 1).

Species composition data was collected in the plots at peak biomass during spring (March–April) of 2022 and 2023 using point-intercept methods along three transects within each plot. The transects were located at 25, 75, and 125 cm distances with respect to the bottom of the 1.5-m axis of the plot. We recorded species identities at 10-cm intervals along each transect while

Figure 1. Example of a litter removal plot in fall immediately after raking (left) and a litter removal plot in spring during sampling (right). Stakes were permanently installed but polyvinyl chloride (PVC) quadrats were removed after raking and sampling for each plot.

traversing the 3-m axis of each plot (totaling to 90 points per plot). "Hits" were recording by lowering a marking flag and noting all species that contacted the wire. For each point, the soil surface cover was recorded (any soil surface not covered in litter, meaning senesced plant matter of any species, was considered "bare ground" which included loose sandy soil, gopher holes, and rock).

To contextualize our results, we extracted daily precipitation data for the city of Riverside to calculate mean growing season precipitation (October 1–May 31) for each of our study years from the Applied Climate Information System (Regional Climate Centers 2013).

Statistical Analyses

Litter Response to Raking. Before testing our hypotheses, we first examined the efficacy of the raking treatment in reducing litter cover by calculating the percentage of the soil surface covered in litter for each plot. While this only captures the recumbent litter close to the ground and not the standing litter which is most likely to reduce light availability and thus alter species composition, we used this metric of litter cover as a proxy to test if the raking treatments were effective in altering litter. To test the effect of the raking treatment on litter, we fit a linear mixed model with the interaction between treatment and year (coded as a categorical variable) as a fixed effect. Since we expected that litter production will vary among years due to interannual differences in precipitation amount (Dudney et al. 2017), to isolate the treatment effect on litter we included the 2021 baseline year data in our models and tested the statistical significance of the interaction of treatment and year to determine if the treatment altered litter levels over background variation in the system. To account for spatial heterogeneity across the site, block was fit as a random effect; to account for repeated observations of plots across years, we fit plot ID nested within block as a random effect.

H1: Functional Group Responses to Litter Removal. To test our first hypothesis—that litter removal will increase native species and exotic forb species abundance, richness, and diversity, we first tested the effect of litter removal on native and exotic forb group abundance. To calculate these quantities, we summed all hits of living plant matter in all three transects within each plot, calculated relative abundance for each species, and summed the relative abundances of the species in each functional group. Species that were present in a plot but did not intersect a transect were added as one hit to the total hits for each plot. We lumped unknown species with congeners to address unresolved species identifications (which comprised less than 0.001% of the hits in our dataset). To analyze functional group abundance, we used relative abundances rather than absolute cover because the cover of native forbs, exotic forbs, and exotic grasses can significantly vary among years in this system due to differences in annual precipitation (Minnich 2008; Elmendorf & Harrison 2009). Relativizing abundance allowed us to test how the treatments affect competitive dynamics between these groups while reducing the influence of variation due to precipitation on our inferences.

We fit global models across all years and treatments in which treatment, year, and the interaction of treatment and year were fit as fixed effects (Supplements S3 and S4). Similarly to the mixed model for litter cover, to account for spatial heterogeneity in species composition across the site, block was fit as a random effect; to account for repeated observations of plots across years, we fit plot ID nested within block as a random effect. To isolate the treatment effect on group abundances, we included the 2021 baseline year data in our models and tested the statistical significance of the interaction of treatment and year. We used this approach to test our hypothesis because we expect functional group abundances to vary among years regardless of treatment due to interannual variation in precipitation; this approach allowed us to test if the treatment altered group abundance over background variation in the system.

We also tested for the effect of litter removal within years (i.e., compared treatments to controls in the same year) to assess effects that were not robust enough to be significant in the global model. In these single-year models, only block was included as a random effect due to the absence of repeated measurements, and treatment was the only fixed effect. For each single-year model, we tested if the response variable significantly differed between treatment and control plots, and then compared these results to the global models to assess which effects were robust enough to be significant in both global and single-year models.

H1: Exotic Grass Response to Litter Removal. Next, we assessed whether the raking treatment alters native forb abundance by reducing the direct impacts of litter (e.g., reduction in light availability), or by reducing competition from live exotic grasses, as there is evidence that exotic grass growth and abundance can be promoted by conspecific litter (Molinari & D'Antonio 2020). To do this, we examined the influence of litter removal on the dominant litter-producing species, *B. diandrus*, by testing if litter removal significantly reduces *B. diandrus* absolute areal cover in treatment plots compared to control plots in the treatment years (2022 and 2023). Then, to assess whether living *B. diandrus* had an effect on native species, we tested if live *B. diandrus* absolute cover was correlated with native species absolute cover across all plots using a linear mixed model. We used absolute cover of *B. diandrus* in these analyses rather than relative abundance as a higher relative abundance for one group necessarily means a lower relative abundance for the other group. Thus, analyzing absolute cover allowed us to test if live *B. diandrus* was associated with reduced native forb cover, implying that exotic grasses excluded rather than co-occurred with native forbs growing under the canopy of *B. diandrus*.

H1: Community Diversity Response to Litter Removal. To test the second part of H1—that changes in native and exotic forb abundance and diversity will drive increases in overall community species diversity—we tested the effect of litter removal on multiple metrics of species diversity: species richness, native species richness, Shannon diversity, and Shannon diversity of native species. Similarly to our analysis of functional group abundance, for the reasons described above, we fit global models with the interaction of treatment and year as fixed effects and with plot nested within block as a random effect. We additionally fit single-year models to test the effect of litter removal on the diversity metrics, also as described above. Due to the low number of exotic forb species on average (mean = 1.16), species richness and Shannon diversity were not analyzed for the exotic forb subset of the community.

H2: Community Composition Response to Litter Removal.

Finally, to test if litter removal shifts community composition toward a state with more native and exotic forbs, we analyzed multivariate species composition. We first visualized differences in overall species composition using nonmetric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity among plots (Beals 1984). We then tested for the effect of the interaction of treatment and year on species composition using permutational multivariate analysis of variance (PERMANOVA) computed on a matrix of Bray–Curtis dissimilarity to assess location effects (Anderson 2001). The Bray–Curtis dissimilarity matrix was used for taxonomic composition data because this type of data is continuous and numerical, and because Bray–Curtis dissimilarity does not group samples by shared zeros (shared zeros are common in taxonomic data). We also considered dispersion effects by assessing differences in beta dispersion (Anderson et al. 2006) among the six treatment-year groups (e.g., 2021 unraked plots, 2022 raked plots, etc.) using a permutation test for multivariate homogeneity of group dispersions (Anderson 2006). We then used indicator species analysis to test which species are driving differences in community composition (Dufrene & Legendre 1997). We performed indicator species analyses grouping using the six treatment-year groups, separately for each treatment year with grouping by treatments, and pooling across the treatment years with grouping by treatment.

Additionally, we assessed the effect of litter removal on the composition of the native species subset of the community by conducting the aforementioned analyses of multivariate species composition for only the native species community. To fit the PERMANOVA, plots with zero native species present were excluded and only plots with a nonzero abundance of native species were analyzed in the PERMANOVA, beta dispersion, and indicator species analyses. Due to the low number of exotic forb species in total ($n = 5$) multivariate species composition of exotic forbs was not analyzed.

All analyses were conducted in R version 4.3.3 (R Core Team 2019). Before fitting mixed models for the diversity and functional group abundance metrics, we first conducted data exploration following Zuur et al. (2010), Zuur & Ieno (2016) (see Supplement S1), and Bolker et al. (2009). Observed means, standard errors, and standard deviations by treatment and year for all variables analyzed are shown in Figure S3. Mixed models were fit using the package *lme4* (Bates et al. 2015) for models assuming normal and Poisson-distributed response variables and using the package *glmmTMB* (Brooks et al. 2017) for models with zero-inflation terms and assuming beta-distributed response variables (see also Damgaard & Irvine 2019). Assumed distributions were selected using the package *fitdistrplus* (Delignette-Muller & Dutang 2015). Predicted values from the models with categorical predictors were calculated using the package *emmeans* (Lenth et al. 2024) and visualized with *sjPlot* (Lüdecke 2023). Model validation was conducted using the packages *performance* (Lüdecke et al. 2021) and *DHARMa* (Hartig & Lohse 2022). To test the significance of model terms, we used type II Wald chi-square tests computed using the package *car* (Fox et al. 2012). See Supplements S2 and S3 for more detail on our model fitting, validation, and testing procedure. We used the package *vegan* (Oksanen et al. 2013) to calculate the species diversity and composition metrics as well as to conduct the PERMANOVA, beta dispersion, and indicator species analyses.

Results

Effectiveness of Treatment

We found that raking effectively reduced litter cover (treatment by year interaction, $p < 0.001$) with a difference in litter cover between treatment and control plots of 50.7% in 2022 and 63.6% in 2023 (Fig. S2). However, even with raking, litter cover occupied a substantial portion of the soil surface, with treatment plots having an average of 31.8% litter cover. Because litter cover was not different between historically raked and unraked plots in 2021, we conclude that since past use of the site ended in 2015, litter cover has returned to baseline levels of litter representative of unmanipulated invaded CSS at the experiment site.

H1: Effect of Litter Removal on Functional Group Abundances and Community Diversity

Across all plots, we recorded 22 species, of which 20 were herbaceous, one was a native shrub, and one was a native succulent (see Table S1 for a complete species list). Plot-level species richness ranged from 1 to 11 species with a mean of 4.4 and a median of 4. Precipitation varied among years with 111 mm falling in the 2020–2021 growing season, 123 mm in the 2021–2022 growing season, and 338 mm in the 2022–2023 growing season. Correspondingly, we found that species richness, native species richness, Shannon diversity, exotic forb abundance, and native forb abundance varied among years, as indicated by the global models (Fig. 2, Table 1).

We found a significant treatment by year interaction for exotic forb abundance and Shannon diversity, but did not find a significant interaction for native Shannon diversity, species richness, or native species richness (Fig. 2). Within years in both 2022 and 2023, litter removal significantly increased species richness, Shannon diversity, native forb abundance, and exotic forb abundance compared to the control (Fig. 2). Notably, the effect of litter removal on species richness and native forb abundance was not significant in the global models. Additionally, the effect size of the increase in native forbs and exotic forbs was small; on average across the treatment years, litter removal increased native forb relative abundance by 4.4% and increased exotic forb relative abundance by 7.0%, on average, compared to control plots. These small magnitudes of change highlight the dominance of exotic grasses in this system even with litter removal (Table 1).

Additionally, we found that litter removal significantly reduced the live areal cover of the dominant litter-producing invasive grass at our site, *B. diandrus*, in both treatment years (Fig. 3A, 2022 and 2023). Interestingly, we found no correlation between live *B. diandrus* areal cover and native forb areal cover across all plots in all years (Fig. 3B, $p = 0.922$).

H2: Response of Community Composition to Litter Removal

We found that in the overall community, the treatment significantly altered species composition above interannual variation (Fig. 4; PERMANOVA, treatment by year interaction $p = 0.009$*). Beta dispersion also differed among treatment-year groups (permutational test for beta dispersion among groups, $p = 0.001$*). The indicator species analysis found that across all treatment years in the overall community, the exotic grass *B. diandrus* was indicative of control plots and the following species were indicative of raked plots (Fig. 4; species with asterisks): the exotic forbs *Brassica tournefortii* (Sahara mustard; Brassicaceae) and *Erodium cicutarium* (redstem filaree; Geraniaceae); the native forbs *Amsinckia menziesii* (common fiddleneck; Boraginaceae), *Cryptantha intermedia* (common cryptantha; Boraginaceae), *Lupinus bicolor* (miniature lupine; Fabaceae), and *Calandrinia menziesii* (red maids; Montiaceae); and *Schismus barbatus* (Mediterranean grass; Poaceae). *Schismus barbatus*, an exotic annual grass which is less prevalent than *B. diandrus* at our site (but can be locally common in adjacent south-facing slopes), was also a significant indicator species for litter removal plots in the indicator species analysis for 2023 alone (although this species was not found at all in 2022), suggesting that exotic grasses other than *B. diandrus* can benefit from the removal of litter produced by dominant grass species. In the native forb community, the treatment did not significantly alter species composition (Fig. S4; PERMANOVA, treatment by year interaction p-value $= 0.396$). However, beta dispersion significantly differed among treatment-year groups (permutational test for beta dispersion among groups, $p = 0.022$*). See Supplement S5 for the results of the other indicator species analyses with different groupings and for the native community.

Discussion

Litter production is known to be a mechanism by which invasive species impact natives (D'Antonio & Vitousek 1992; Eppinga et al. 2011; Wainwright et al. 2017), and the importance of this mechanism has been documented in California annual grasslands and CSS (Chen et al. 2018; Molinari & D'Antonio 2020; Charles et al. 2022). However, how litter removal, a potential restoration tool to promote native species, alters the abundances of native forbs compared to exotic forbs and how these changes alter whole-community diversity and structure is less well understood. Here, we found, partly consistent with our first hypothesis, that litter removal increased exotic forb abundance but had a weak positive effect on native forb abundance and overall species richness. These changes resulted in a community state with higher Shannon diversity and a composition with more native and exotic forb species. Overall, our study adds to the body of literature in California herbaceous systems demonstrating that litter produced by exotic grasses inhibits native forbs (Coleman & Levine 2007; Mariotte et al. 2017; Nguyen et al. 2024), and that litter can be an important driver of plant community structure in herbaceous systems (Loydi et al. 2013).

The Role of Litter in Controlling Functional Group Abundance

Our results suggest that litter removal can increase native forb abundance. However, this effect was weak in magnitude compared to background variation among years that was likely driven by interannual variation in precipitation. Stronger in magnitude was the increase in exotic forb abundance with litter removal. This result is consistent with other studies that suggest that controlling both live exotic grass and litter promotes exotic forbs in California herbaceous systems (Allen et al. 2005; Brandt & Seabloom 2012; Cox & Allen 2008; but see Coleman & Levine 2007).

Also consistent with findings from other studies, we found that litter removal effectively reduced the cover of living dominant exotic grasses (Coleman & Levine 2007; Charles et al. 2022; Nguyen et al. 2024). However, this reduction in the live cover of the dominant exotic grass *B. diandrus* was not associated with an increase in native forb cover. This finding is consistent with at least one other study (Molinari & D'Antonio 2020), which found that the presence or abundance of living *B. diandrus* had no effect on native forb abundance in a seed addition experiment. However, there is still reason to suspect that live exotic grass may negatively affect native forbs via mechanisms unrelated to litter cover, as other studies have found that the removal of live exotic grass via either weeding (Coleman & Levine 2007; Thomson et al. 2016) or herbicide (Allen et al. 2005) increased native forb cover (but see HilleRisLambers et al. 2010). Further, it is possible that we observed no effect of live grass on native forbs due to the functional strategies of the native forbs in our species pool, as there is evidence that the effects of live grass on native forb abundance differ based on species functional strategies, with acquisitive native forbs being affected by live grass and conservative native forbs experiencing no effect (LaForgia 2021). Nonetheless, our results highlight the importance of invasive grass litter in suppressing native forbs.

Litter Removal Effects on Plant Community Structure and Potential as a Restoration Tool

We found that the increases in forb abundance driven by litter removal in turn increased community Shannon diversity primarily by increasing species evenness, rather than increasing species richness. While we found that litter removal slightly increased species richness, this increase was dwarfed by the magnitude of variation in species richness among years. Consistent with the fact that species richness is highly variable in this system due to interannual precipitation variability (Elmendorf & Harrison 2009), overall species richness varied interannually even in control plots. For example, richness increased in just 2 years from about 3.2 species in 2021 control

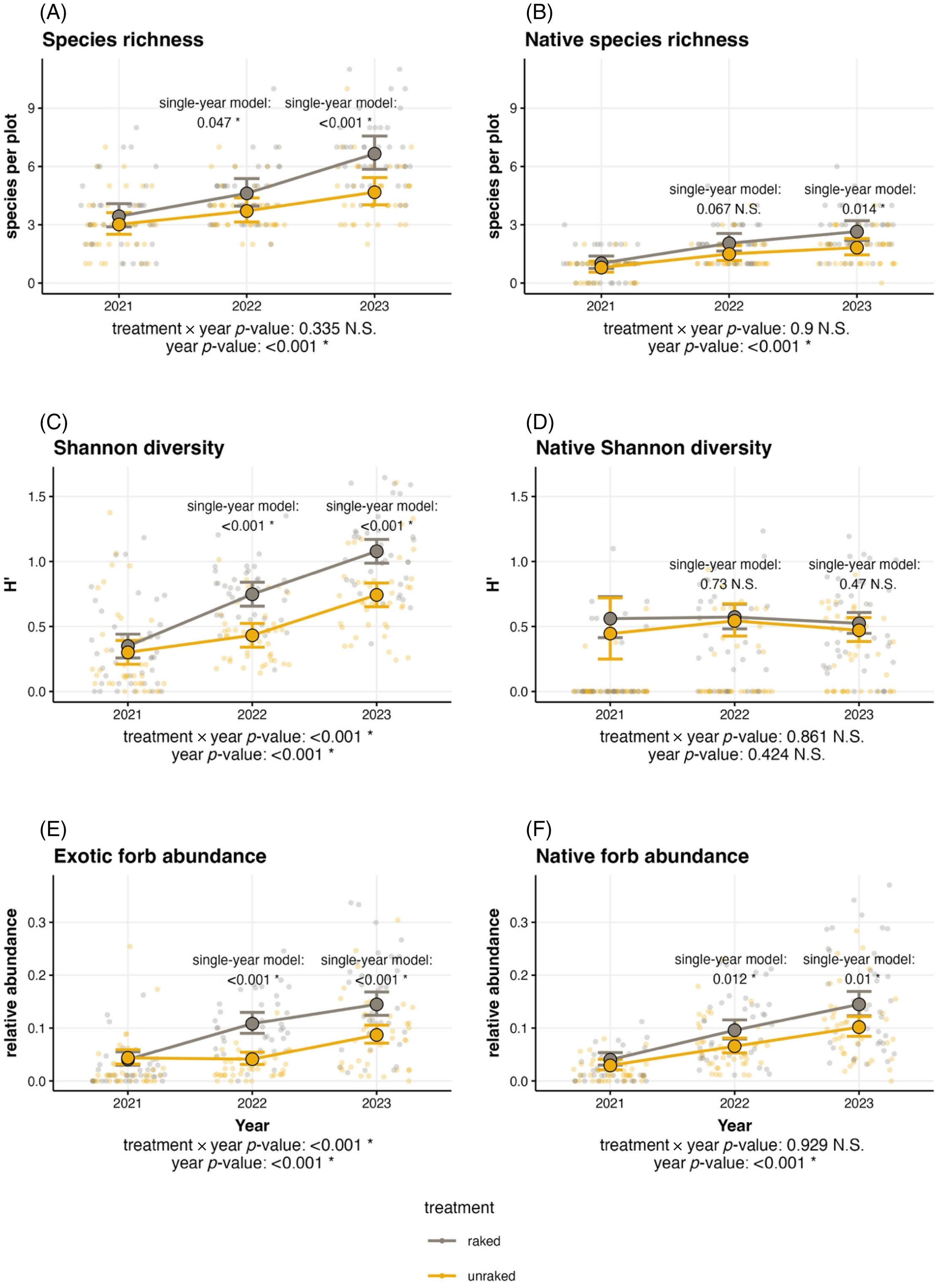

Figure 2. Predicted means (black outlined points) with 95% CI from linear mixed-effects models assessing the effect of treatment, year, and their interaction on (A) species richness (number of species per plot), (B) native species richness, (C) Shannon diversity, (D) Shannon diversity of native species, (E) exotic forb relative abundance, and (F) native forb relative abundance. Points in the background are observed data (horizontally jittered to aid viewing). Gray points represent plots that were sampled in 2021 before litter removal, and then subjected to litter removal prior to the 2022 and 2023 growing seasons; yellow points represent plots that were not manipulated. Also shown for each year are *p*-values from models assessing differences between litter removal and control plots within 2022 and 2023, the years when the treatment was applied.

Table 1. Test statistics and p-values for linear mixed-effects models assessing the effect of litter removal treatment, year, and their interaction on multiple metrics of plant community structure: species richness (number of species per plot), native species richness, Shannon diversity, Shannon diversity of native species, exotic forb relative abundance, and native forb relative abundance.

Response Variable	*Model Type*	*Predictor*	*Year*	*Degrees of Freedom*	χ^2	p
Overall species richness	Global	Treatment		1	16.71	<0.001*
	Global	Treatment:year		2	2.19	0.335
	Global	Year		2	54.95	<0.001*
	Single-year	Treatment	2022	1	3.93	0.047*
	Single-year	Treatment	2023	1	13.83	<0.001*
Native species richness	Global	Treatment		1	10.27	0.001*
	Global	Treatment:year		2	0.21	0.9
	Global	Year		2	41.72	<0.001*
	Single-year	Treatment	2022	1	3.36	0.067
	Single-year	Treatment	2023	1	6.01	0.014*
Shannon diversity index	Global	Treatment		1	65.06	<0.001*
	Global	Treatment:year		2	24.12	<0.001*
	Global	Year		2	322.72	<0.001*
	Single-year	Treatment	2022	1	52.84	<0.001*
	Single-year	Treatment	2023	1	61.63	<0.001*
Shannon diversity index of native species (log-transformed)	Global	Treatment		1	0.96	0.327
	Global	Treatment:year		2	0.3	0.861
	Global	Year		2	1.72	0.424
	Single-year	Treatment	2022	1	0.12	0.73
	Single-year	Treatment	2023	1	0.53	0.47
Native forb relative abundance	Global	Treatment		1	11.87	<0.001*
	Global	Treatment:year		2	0.15	0.929
	Global	Year		2	126.76	<0.001*
	Single-year	Treatment	2022	1	6.24	0.012*
	Single-year	Treatment	2023	1	6.57	0.01*
Exotic forb relative abundance	Global	Treatment		1	39.11	<0.001*
	Global	Treatment:year		2	16.82	<0.001*
	Global	Year		2	62.06	<0.001*
	Single-year	Treatment	2022	1	95.11	<0.001*
	Single-year	Treatment	2023	1	18.82	<0.001*

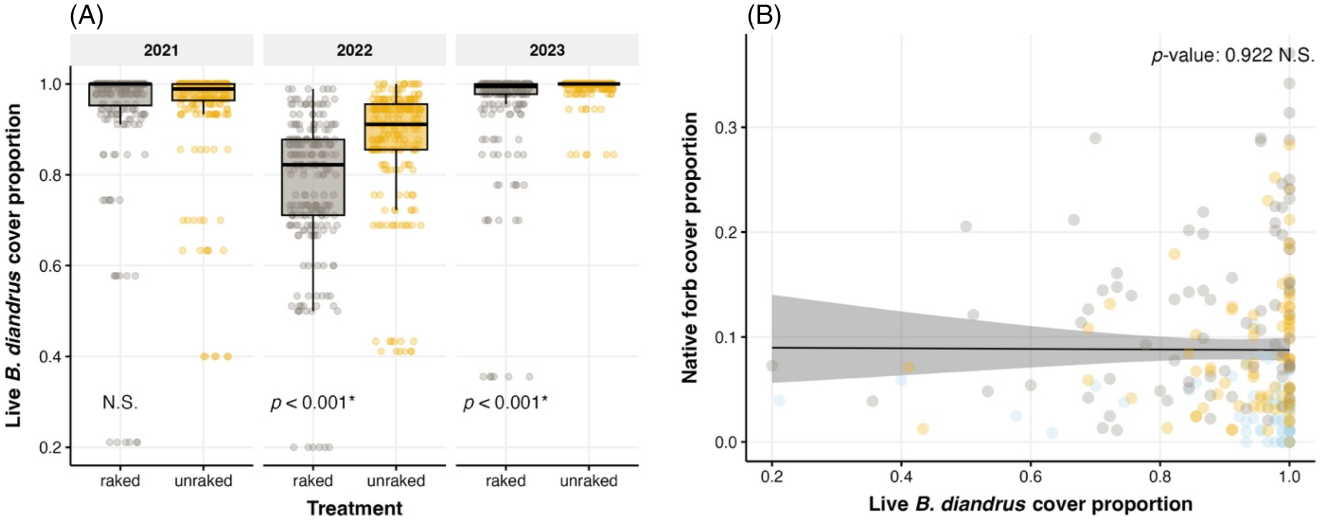

Figure 3. Panel (A) shows the effect of litter removal on live *Bromus diandrus* cover in the treatment years of 2022 and 2023. Panel (B) shows the association of live *Bromus diandrus* cover with native forb cover. The black line with confidence interval shows model predictions from a mixed model. Blue points show plots in the baseline year of 2021 where no treatments were applied, yellow points represent control plots in 2022 and 2023, and gray points represent litter removal plots in 2022 and 2023.

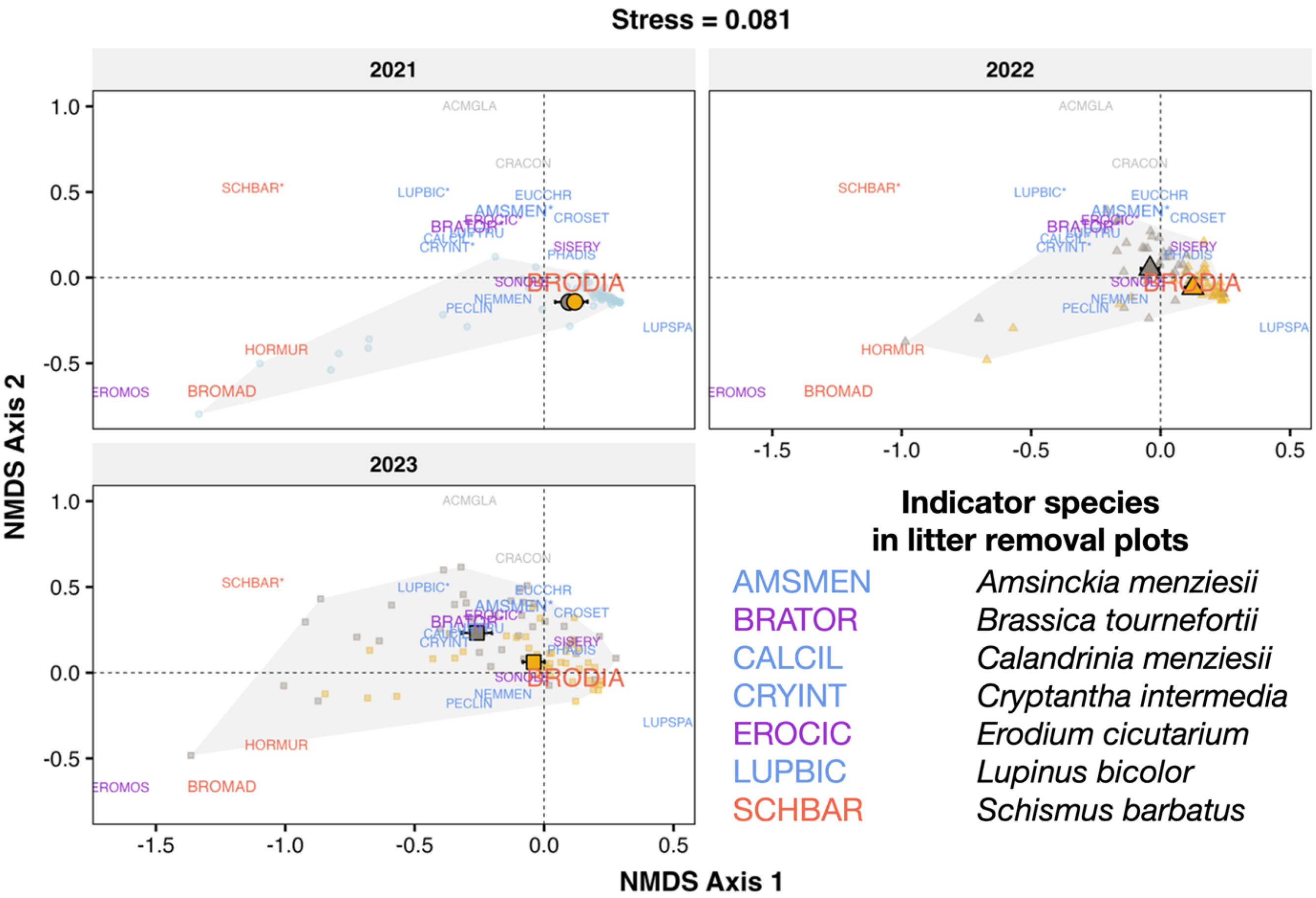

Figure 4. Nonmetric multidimensional scaling (stress = 0.081) of the overall community separated by each year. Each black-outlined point represents mean NMDS scores (±SE) for plots within each treatment-year group with convex hulls and shapes (triangle, circle, or square) for each year. Each transparent point represents the NMDS scores for an individual plot (blue points are plots prior to litter removal, gray points are plots after litter removal, and yellow points are control plots). Points that are closer together are more similar in species composition. The species codes represent NMDS scores for individual species and are colored based on the species provenance and growth form (red = exotic grasses, blue = native forbs, purple = exotic forbs, gray = native shrub and native succulent) and the size of the text corresponds to the relative abundance of the species across all plots and years in our study. Asterisks denote species that were indicators of treatment plots across 2022 and 2023. The codes for nonindicator species are as follows: ACMGLA, *Acmispon glaber* (Fabaceae); BRODIA, *Bromus diandrus*; BROMAD, *Bromus madritensis* (Poaceae); CRACON, *Crassula connata* (Crassulaceae); CROSET, *Croton setigerus* (Euphorbiaceae); EROMOS, *Erodium moschatum* (Geraniaceae); EUCCHR, *Eucrypta chrysanthemifolia* (Hydrophyllaceae); HORMUR, *Hordeum murinum* (Poaceae); LUPSPA, *Lupinus sparsiflorus*; LUPTRU, *Lupinus truncatus* (Fabaceae); NEMMEN, *Nemophila menziesii* (Hydrophyllaceae); PECLIN, *Pectocarya linearis* (Boraginaceae); PHADIS, *Phacelia distans* (Hydrophyllaceae); SISERY, *Sisymbrium erysimoides* (Brassicaceae); SONOLE, *Sonchus oleraceus* (Asteraceae).

plots to 4.7 species in 2023 control plots. This difference is likely explained by the differences in precipitation among years as 2021 was a relatively dry year, 2022 was slightly wetter, and 2023 was a very wet year, compared to the mean annual precipitation for the area. Compared to this magnitude of change in species richness among years, the greatest effect of litter removal on overall species richness is relatively small, with raked plots having 2.0 more species on average than control plots in 2023. Despite the small magnitude of this effect, however, our result is consistent with observations that patches dominated by *B. diandrus* exhibit lower species richness and Shannon diversity than native grass-dominated patches in California annual grassland (Molinari & D'Antonio 2014). Our results provide evidence that litter is a mechanism by which exotic grasses reduce species richness and Shannon diversity in California herbaceous systems. These effects of litter on community structure were further supported by our multivariate analysis, where we found that treatment and control communities differed in their species composition and beta diversity. The differences between communities were primarily driven by native forbs and the exotic forbs *E. cicutarium* and *B. tournefortii*, the latter of which is considered highly invasive in California (California Invasive Plant Council n.d.).

Importantly, we found that litter removal did not change the diversity or composition of the native species in the community. Specifically, litter removal did not increase native species richness or Shannon diversity, suggesting that litter removal alters community composition primarily by increasing the abundance of native and exotic forbs already present and co-occurring with grasses, and not by the addition of new native species. This finding is in contrast with a study in a more mesic California coastal meadow system which found that litter removal increased native forb and exotic forb species richness (Coleman & Levine 2007), suggesting that the impact of litter removal on community diversity may be mediated by local environmental conditions.

Taken together, our results suggest that litter removal can present a trade-off between controlling exotic grass invaders and controlling exotic forb invaders, at least in this CSS system, and may be applicable to other California herbaceous ecosystems that share many of the same species. Litter removal may be an appropriate intervention if managing for increased plant species diversity, greater native forb cover to provide resources for pollinators and improve the aesthetic value of landscapes (Lesage et al. 2018), as well as reduced invasive grass cover for fire hazard mitigation (Hernández et al. 2019) and wildlife habitat (Bowler 2000). However, if the land management goal is to increase native forb cover without promoting exotic forb invaders, then other interventions or a combination of litter removal and other treatments may be more appropriate. Further, methods to remove litter other than raking may be more scalable such as grazing (Beck et al. 2015; Lesage et al. 2022) and prescribed fire (Gillespie & Allen 2004) although these interventions will likely have distinct effects compared to manual litter removal. Nevertheless, our results suggest that at this spatial scale, litter removal can move communities to a more diverse state with a greater abundance of native and exotic forbs, and that litter removal can be an effective treatment to increase native forb abundance even without concurrent seed addition treatments. It is widely accepted that restoration in this system may not be able to return CSS to its historic state, but rather may be able to move invaded CSS to a more diverse novel state with both native and exotic species (Bell et al. 2016; Cleland et al. 2016). Our study highlights the potential of litter removal to achieve this goal.

Suggested Future Directions for Research

To advance our understanding of the efficacy of litter removal in restoring native herbaceous species in California as well as in other regions, we suggest some topics for further work. While our study found that litter removal altered species composition, the mechanism by which particular species were promoted is unclear. Further work could explore whether litter removal promotes species with smaller seed mass (Amatangelo et al. 2008; Chen et al. 2018; but see Charles et al. 2022). Additionally, further studies should examine the effects of multi-year litter removal on species diversity and composition, which will also help us understand several dynamics that shape community trajectories which were not captured in our study. For example, if litter removal is continued over many years, random dispersal could allow new native or exotic species from surrounding areas to colonize in the absence of litter-mediated exotic grass competition, thereby increasing species richness. Long-term studies could also examine how interannual variation in precipitation interacts with litter removal to control species composition and diversity. Precipitation variability is known to mediate grass-shrub interactions in CSS (Goldstein & Suding 2014) and grass-forb competition in California annual grasslands (Minnich 2008; LaForgia et al. 2020), and lag effects due to litter accumulation from preceding years with high precipitation have been found to reduce forb abundance (Dudney et al. 2017). Further work could elucidate the extent to which litter removal disrupts lag effects to alter the temporal stability of forb cover. Finally, future long-term studies could determine if increasing exotic and native forb abundance compounds over multiple years as seedbanks develop, and if such dynamics can lead to an alternative stable state (Beisner et al. 2003) that is resistant to grass invasion.

Further work could also employ a functional traits approach to improve restoration outcomes by informing the selection of native species in restoration projects that can compete with exotic forb species that may replace exotic grasses under litter removal. Multiple studies have explored the evolutionary history that may explain the potential competitive superiority of exotic forbs over native forbs (Cadotte et al. 2010; HilleRisLambers et al. 2010; Galán Díaz et al. 2023) and other studies suggest that traits mediate the performance of native and exotic species in invaded annual grasslands at multiple demographic stages (Molinari & D'Antonio 2014; LaForgia 2021; Charles et al. 2022). Some have suggested a competitive hierarchy where exotic grasses outcompete exotic and native forbs, but where the magnitude of competitive advantage for exotic forbs over native forbs is weaker (Allen et al. 2005; Cox & Allen 2011). Thus, trait-based approaches may be fruitful to identify native forb species from the regional species pool that can persist under exotic forb competition. Ideal native species for successful restoration projects would be competitive in both high litter and low litter environments, given interannual variability in litter production in California annual grassland and CSS systems as well as the possibility that litter reduction interventions are not consistently applied due to logistical constraints. While restoration to historic states may be out of reach, management may be able to promote novel assemblages that maintain higher levels of plant diversity.

Acknowledgments

We thank the undergraduate students of the Ecological Society of America's Strategies for Ecology Education, Diversity, and Sustainability (SEEDS) Chapter at the University of California–Riverside and graduate students in the Center for Conservation Biology at the University of California—Riverside, for assistance with fieldwork and data entry. We especially thank C. Nguyen, C. Cosma, D. Yen, L. Rouzaud, B. Taga, G. Chavez, T. Nair, C. Daley, A. Huynh, G. Shen, K. Morales, J. Fuerte, and J. Choi for help with fieldwork. We also thank K. Anderson and D. Jenerette for logistical support; A. Sanders of the UCR Herbarium for assistance with species identification; T. Madsen-Hepp, L. Larios, J. Henn, K. Suding, and C. White for helpful comments and assistance with analyses; and the Spasojevic and Suding Lab groups for helpful feedback on the manuscript. We thank the Sea & Sage Chapter of the Audubon Society (Irvine, CA) and the University of California—Riverside Center for Conservation Biology for financial support. This material is based on work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE 2040434. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

DATA AVAILABILITY STATEMENT

The plant community composition data that support the findings of this study are openly available in Dryad at Ramachandran et al. (2024). All R code used to process and analyze the data in this study are openly available on Zenodo and GitHub at https://doi.org/10.5281/zenodo.14089394.

LITERATURE CITED

Allen EB, Cox RD, Tennant T, Kee SN, Deutschman D (2005) Landscape restoration in southern California forblands: response of abandoned farmland to invasive annual grass control. Israel Journal of Plant Sciences 53:237–245. https://doi.org/10.1560/65LM-55YH-GB49-5BJM

Amatangelo KL, Dukes JS, Field CB (2008) Responses of a California annual grassland to litter manipulation. Journal of Vegetation Science 19:605–612. https://doi.org/10.3170/2008-8-18415

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62:245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01

Beals EW (1984) Bray-Curtis ordination—an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1–55. https://doi.org/10.1016/S0065-2504(08)60168-3

Beck JJ, Hernández DL, Pasari JR, Zavaleta ES (2015) Grazing maintains native plant diversity and promotes community stability in an annual grassland. Ecological Applications 25:1259–1270. https://doi.org/10.1890/14-1093.1

Beisner B, Haydon D, Cuddington K (2003) Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382. https://doi.org/10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2

Bell CE, Allen EB, Weathers KA, McGiffen M (2016) Simple approaches to improve restoration of coastal sage scrub habitat in southern California. Natural Areas Journal 36:20–28. https://doi.org/10.3375/043.036.0107

Benitez L, Kendig AE, Adhikari A, Clay K, Harmon PF, Holt RD, Goss EM, Flory SL (2022) Invasive grass litter suppresses a native grass species and promotes disease. Ecosphere 13:e3907. https://doi.org/10.1002/ecs2.3907

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bowler PA (2000) Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. Environmental Management 26:S85–S96. https://doi.org/10.1007/s002670010064

Brandt AJ, Seabloom EW (2012) Seed and establishment limitation contribute to long-term native forb declines in California grasslands. Ecology 93:1451–1462. https://doi.org/10.1890/11-0579.1

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400. https://doi.org/10.32614/RJ-2017-066

Cadotte MW, Borer ET, Seabloom EW, Cavender-Bares J, Harpole WS, Cleland E, Davies KF (2010) Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in northern California. Diversity and Distributions 16:892–901. https://doi.org/10.1111/j.1472-4642.2010.00700.x

California Invasive Plant Council (n.d.) *Brassica tournefortii Profile*. https://www.cal-ipc.org/plants/profile/brassica-tournefortii-profile/ Accessed 2024-04-21 09:35:59

Charles LS, Maron JL, Larios L (2022) Species provenance and traits mediate establishment and performance in an invaded grassland. Functional Ecology 36:1528–1541. https://doi.org/10.1111/1365-2435.14044

Chen B-M, D'Antonio CM, Molinari N, Peng S-L (2018) Mechanisms of influence of invasive grass litter on germination and growth of coexisting species in California. Biological Invasions 20:1881–1897. https://doi.org/10.1007/s10530-018-1668-5

Cleland EE, Funk J, Allen EB (2016) Coastal sage scrub. Pages 429–448. In: Zavaleta E, Mooney H (eds) Ecosystems of California. University of California Press, Berkeley, California

Coleman HM, Levine JM (2007) Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. Biological Invasions 9:65–71. https://doi.org/10.1007/s10530-006-9008-6

Cox RD, Allen EB (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. Journal of Applied Ecology 45:495–504. https://doi.org/10.1111/j.1365-2664.2007.01437.x

Cox RD, Allen EB (2011) The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland. Plant Ecology 212:1699–1707. https://doi.org/10.1007/s11258-011-9942-y

Damgaard CF, Irvine KM (2019) Using the beta distribution to analyse plant cover data. Journal of Ecology 107:2747–2759. https://doi.org/10.1111/1365-2745.13200

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Delignette-Muller ML, Dutang C (2015) fitdistrplus: an R package for fitting distributions. Journal of Statistical Software 64:1–34. https://doi.org/10.18637/jss.v064.i04

Dudney J, Hallett LM, Larios L, Farrer EC, Spotswood EN, Stein C, Suding KN (2017) Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? Journal of Ecology 105:484–495. https://doi.org/10.1111/1365-2745.12671

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366. https://doi.org/10.2307/2963459

Elmendorf SC, Harrison SP (2009) Temporal variability and nestedness in California grassland species composition. Ecology 90:1492–1497. https://doi.org/10.1890/08-1677.1

Eppinga MB, Kaproth MA, Collins AR, Molofsky J (2011) Litter feedbacks, evolutionary change and exotic plant invasion. Journal of Ecology 99:503–514. https://doi.org/10.1111/j.1365-2745.2010.01781.x

Eviner VT (2016) Grasslands. Pages 449–478. In: Zavaleta E, Mooney H (eds) Ecosystems of California. University of California Press, Berkeley, California

Facelli JM, Pickett STA (1991) Plant litter: its dynamics and effects on plant community structure. The Botanical Review 57:1–32. https://doi.org/10.1007/BF02858763

Farrer EC, Goldberg DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. Ecological Applications 19:398–412. https://doi.org/10.1890/08-0485.1

Foster BL, Gross KL (1998) Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology 79:2593–2602. https://doi.org/10.1890/0012-9658(1998)079[2593:SRIASG]2.0.CO;2

Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S (2012) Package "car". R Foundation for Statistical Computing, Vienna, Austria. https://cran.uni-muenster.de/web/packages/car/car.pdf Accessed 2024-02-19

Galán Díaz J, Vilà M, Parker IM, de la Riva EG (2023) Functional assembly of grassland plant species in native communities in Spain and recipient communities in California. Journal of Ecology 111:214–226. https://doi.org/10.1111/1365-2745.14027

Gillespie IG, Allen EB (2004) Fire and competition in a southern California grassland: impacts on the rare forb *Erodium macrophyllum*. Journal of Applied Ecology 41:643–652. https://doi.org/10.1111/j.0021-8901.2004.00935.x

Goldstein LJ, Suding KN (2014) Intra-annual rainfall regime shifts competitive interactions between coastal sage scrub and invasive grasses. Ecology 95: 425–435. https://doi.org/10.1890/12-0651.1

Hartig F, Lohse L (2022) *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models*. https://cran.r-project.org/web/packages/DHARMa/index.html Accessed 2024-02-19

Hernández E, Questad EJ, Meyer WM, Suding KN (2019) The effects of nitrogen deposition and invasion on litter fuel quality and decomposition in a *Stipa pulchra* grassland. Journal of Arid Environments 162:35–44. https://doi.org/10.1016/j.jaridenv.2018.11.003

HilleRisLambers J, Yelenik SG, Colman BP, Levine JM (2010) California annual grass invaders: the drivers or passengers of change? Journal of Ecology 98: 1147–1156. https://doi.org/10.1111/j.1365-2745.2010.01706.x

Jepson Flora Project (2024) *Jepson eFlora*. https://ucjeps.berkeley.edu/eflora Accessed 2024-04-21

Kortessis N, Kendig AE, Barfield M, Flory SL, Simon MW, Holt RD (2022) Litter, plant competition, and ecosystem dynamics: a theoretical perspective. The American Naturalist 200:739–754. https://doi.org/10.1086/721438

LaForgia ML (2021) Impacts of invasive annual grasses and their litter vary by native functional strategy. Biological Invasions 23:2621–2633. https://doi.org/10.1007/s10530-021-02527-2

LaForgia ML, Harrison SP, Latimer AM (2020) Invasive species interact with climatic variability to reduce success of natives. Ecology 101:e03022. https://doi.org/10.1002/ecy.3022

Lenth, RV, Bolker, B, Buerkner, P, Giné-Vázquez, I, Herve, M, Jung, M, Love, J, Miguez, F, Riebl, H, & Singmann, H (2024) emmeans: estimated marginal means, aka least-squares means (1.10.1) [Computer software]. https://doi.org/10.32614/CRAN.package.emmeans

Lenz TI, Moyle-Croft JL, Facelli JM (2003) Direct and indirect effects of exotic annual grasses on species composition of a south Australian grassland. Austral Ecology 28:23–32. https://doi.org/10.1046/j.1442-9993.2003.01238.x

Lesage JC, Hayes GF, Holl KD (2022) Native annual forbs decline in California coastal prairies over 15 years despite grazing. PLoS One 17:e0278608. https://doi.org/10.1371/journal.pone.0278608

Lesage JC, Howard EA, Holl KD (2018) Homogenizing biodiversity in restoration: the “perennialization” of California prairies. Restoration Ecology 26:1061–1065. https://doi.org/10.1111/rec.12887

Loydi A, Donath TW, Eckstein RL, Otte A (2015) Non-native species litter reduces germination and growth of resident forbs and grasses: allelopathic, osmotic or mechanical effects? Biological Invasions 17:581–595. https://doi.org/10.1007/s10530-014-0750-x

Loydi A, Eckstein RL, Otte A, Donath TW (2013) Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. Journal of Ecology 101:454–464. https://doi.org/10.1111/1365-2745.12033

Lüdecke, D (2023a). *sjPlot: data visualization for statistics in social science* (2.8.15) [Computer software]. https://doi.org/10.32614/CRAN.package.sjPlot

Lüdecke D (2023b) *sjPlot: data visualization for statistics in social science*. https://cran.r-project.org/web/packages/sjPlot/index.html Accessed 2024-02-19

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D (2021) Performance: an R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6:3139. https://doi.org/10.21105/joss.03139

Mariotte P, Spotswood EN, Farrer EC, Suding KN (2017) Positive litter feedbacks of an introduced species reduce native diversity and promote invasion in Californian grasslands. Applied Vegetation Science 20:28–39. https://doi.org/10.1111/avsc.12291

Minnich RA (2008) California’s fading wildflowers: lost legacy and biological invasions. University of California Press, Berkeley, California. https://doi.org/10.1525/9780520934337

Minnich RA, Dezzani RJ (1998) Historical decline of coastal sage scrub in the Riverside-Perris plain, California. Western Birds 29:366–391

Molinari NA, D’Antonio CM (2014) Structural, compositional and trait differences between native- and non-native-dominated grassland patches. Functional Ecology 28:745–754. https://doi.org/10.1111/1365-2435.12206

Molinari NA, D’Antonio CM (2020) Where have all the wildflowers gone? The role of exotic grass thatch. Biological Invasions 22:957–968. https://doi.org/10.1007/s10530-019-02135-1

National Centers for Environmental Information. (2023). *U.S. Climate Normals Quick Access 1991-2020, Station USW00003171 Annual/Seasonal Normals* (v1.0.1) [dataset]. National Centers for Environmental Information. https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals-annualseasonal&timeframe=30&station=USW00003171 Accessed 2024-04-20 15:42:07

Nguyen MA, Kimball S, Burger JC, Freese R, Lulow M, Schmidt KT, Ta P, Funk JL (2024) Applying community assembly theory to restoration: overcoming dispersal and abiotic filters is key to diversifying California grassland. Restoration Ecology 32:e14018. https://doi.org/10.1111/rec.14018

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, et al. (2013) Vegan: community ecology package. R package version 2.6-4. R Foundation for Statistical Computing, Vienna, Austria

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species’ traits and environment. Global Change Biology 18:1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Ramachandran A, Iwanaga C, Fugate M, Huxley J, Rose-Person A, Amatya R, Bui T-T, Spasojevic M (2024) *Plant community composition in response to litter removal in Riverside, Dryad, California, USA*. 2021-2023 [Dataset]. https://doi.org/10.5061/dryad.3xsj3txrj

R Core Team (2019) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria

Regional Climate Centers (2013) *Single station daily data listing, riverside municipal airport*. https://scacis.rcc-acis.org/ Accessed 2024-03-20

Rundel PW (2007) Sage scrub. Pages 208–228. In: Terrestrial vegetation of California. Third edition. University of California Press, Berkeley, California. https://doi.org/10.1525/california/9780520249554.003.0008

Ruprecht E, Szabó A (2012) Grass litter is a natural seed trap in long-term undisturbed grassland. Journal of Vegetation Science 23:495–504. https://doi.org/10.1111/j.1654-1103.2011.01376.x

Thomson DM, Cruz-de Hoyos R, Cummings K, Schultz EL (2016) Why are native annual abundances low in invaded grasslands? Testing the effects of competition and seed limitation. Plant Ecology 217:431–442. https://doi.org/10.1007/s11258-016-0584-y

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Wainwright CE, Dwyer JM, Mayfield MM (2017) Effects of exotic annual grass litter and local environmental gradients on annual plant community structure. Biological Invasions 19:479–491. https://doi.org/10.1007/s10530-016-1303-2

Wolkovich EM, Lipson DA, Virginia RA, Cottingham KL, Bolger DT (2010) Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. Global Change Biology 16:1351–1365. https://doi.org/10.1111/j.1365-2486.2009.02001.x

Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution 7:636–645. https://doi.org/10.1111/2041-210X.12577

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Supporting Information

The following information may be found in the online version of this article:

Table S1. Species list for study site.
Figure S1. Color-coded schematic of the current experimental site.
Figure S2. Litter cover across years and treatments.
Figure S3. Means with standard error (a) and standard deviation (b) for all diversity and group abundance variables analyzed.
Figure S4. Non-metric multidimensional scaling (stress = 0.062) for the native subset of the community.
Supplement S1. Data exploration procedure.
Supplement S2. *Bromus diandrus* cover versus native forb cover analysis procedure.
Supplement S3. Global model selection and fitting procedure.
Supplement S4. Model selection and fitting procedure for individual year models.
Supplement S5. Indicator species analysis results for different groupings.

Coordinating Editor: Michael Sievers

Received: 14 July, 2024; First decision: 27 September, 2024; Revised: 27 October, 2024; Accepted: 29 October, 2024